First evidence for a latitudinal body mass effect in extant Crocodylia and the relationships of their reproductive characters

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Suggested RH – Crocodylian reproductive traits

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Abstract

Relationships between distribution patterns and body size have been documented in many endothermic taxa. However, the evidence for these trends in ectotherms generally is equivocal, and there have been no studies of effects in crocodylians specifically. Here, we examine the relationship between latitudinal distribution and body mass in 20 extant species of crocodylians, as well as the relationships between seven important reproductive variables. Using phylogenetically independent contrasts to inform generalised linear models, we provide the first evidence of a latitudinal effect on adult female body mass in crocodylians. In addition, we explore the relationships between reproductive variables including egg mass, hatchling mass and clutch size. We report no correlation between egg mass and clutch size, upholding previously reported within-species trends. We also find no evidence of a correlation between measures of latitudinal range and incubation temperature, contrasting with the trends found in turtles..

Keywords: *crocodylians; reproduction; generalised linear model; latitude; body size; biogeography*

1 Introduction

The broad impact of climate on the body size of numerous vertebrate and invertebrate groups has been demonstrated across latitudinal (Ray 1960; Wooller et al. 1985; Graves 1991; Kaspari and Vargo 1995; Saunders and Tarling 2018) and altitudinal (Bernadou et al. 2016; Davis and Burtt Jr. 2019; Yu et al. 2019) gradients, insofar as these correlate with temperature gradients. While evidence of latitudinal size gradients is common in endotherms (Ashton 2002a; Blackburn and Hawkins 2004), the effect of latitude on ectotherm body sizes is more controversial (Ashton and Feldman 2003; Pincheira-Donoso et al. 2008). For example, amphibians (Ashton 2002b; Adams and Church 2008), lizards (Ashton and Feldman 2003; Cruz et al. 2005; Pincheira-Donoso et al. 2008) and turtles (Ashton and Feldman 2003; Lindeman 2008; Angielczyk et al. 2015) have all been the subjects of studies with a diversity of findings. Strikingly, however, no previous studies have attempted to test whether this correlated variation applies to another major group of living reptiles, the crocodylians.

Crocodylians are a vital component of their ecosystems, often acting as keystone species in tropical regions (Ashton 2010). They represent the last surviving pseudosuchian archosaurs, a clade that once inhabited every continent and that has persisted for at least 230 Ma (Irmis et al. 2013; Turner et al. 2017). Having survived the devastating Cretaceous-Paleogene (K-Pg) mass extinction (Bronzati et al. 2015; Puértolas-Pascual et al. 2016), as well as a number of other,

smaller or more protracted major extinction events (Hutchison 1982; Markwick 1993; Toljagić and Butler 2013; Mannion et al. 2015), crocodylians have demonstrated remarkable resilience to cataclysmic climate change and habitat loss (Toljagić and Butler 2013). Despite this, half of all extant crocodylian species are currently threatened with extinction and, at the current rate, vertebrate species loss will soon equal or even exceed that of the K-Pg event (Barnosky et al. 2011; Pievani 2014; Lécuyer 2018). To understand possible future trends in crocodylian diversity more fully, it is important that their current diversity, ecology and distribution are fully characterized (Figure 1). Despite previous work in this area (Martin 2007; Pierce et al. 2008; Nicolaï and Matzke 2019), the nature of the relationship between geographical distribution and the reproductive biology of living crocodylians is unclear.

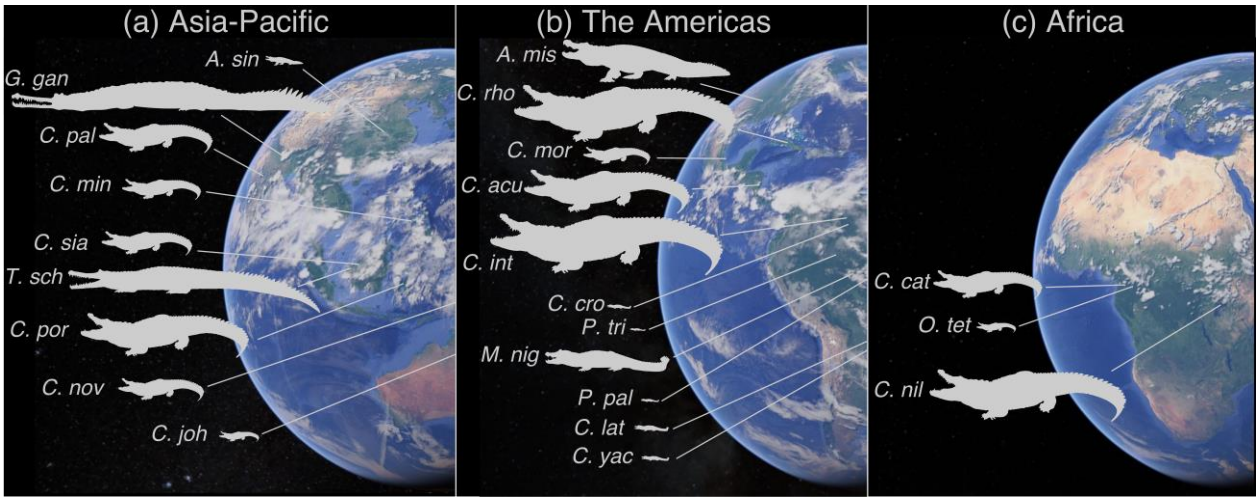

Figure 1. A representation of the relationship between the mean adult female body masses of 23 species of crocodylian and their latitudinal midpoint. Silhouette th scaled to body mass. (a) Asia-Pacific, (b) The Americas, (c) Africa. Abbreviations (Asia-Pacific): Alligator sinensis, Gavialis gangeticus, Crocodylus palustris, Crocodylus mindorensis, Crocodylus siamensis, Tomistoma schlegelii, Crocodylus porosus, Crocodylus novaeguineae, Crocodylus johnstoni. *(Americas):* Alligator mississippiensis,

Crocodylus rhombifer, Crocodylus moreletii, Crocodylus acutus, Crocodylus intermedius, Caiman crocodilus, Paleosuchus trigonatus, Melanosuchus niger, Paleosuchus palpebrosus, Caiman latirostris, Caiman yacare *(Africa):* Crocodylus cataphractus, Osteolaemus tetraspis, Crocodylus niloticus. Mesticops leptorhynchus, Crocodylus suchus *and* Osteolaemus osborni *were excluded due to lack of reliable female mass data.*

The resilience of crocodylians to historic mass extinctions is also much debated. Previous work has implicated many different factors in their survival, including diet (Sheehan and Hansen 1986), aquaticism (Robertson et al. 2013), famine resistance (Robertson et al. 2013), induction of torpor at low air or water temperatures (Almandarz 1975; Brisbin Jr. et al. 1982; Sun et al. 2019) and their propensity to burrow in order to take refuge from harsh environmental conditions (Thorbjarnarson 1989; Mobaraki et al. 2015). Another hypothesis concerns their unique reproductive biology (Charruau et al. 2017). Crocodylians have no sex chromosomes and hatchling sex is thought to be fully controlled by incubation temperature. Temperature dependent sex determination (TSD) systems have a threshold that yields an approximately 1:1 ratio of males and females at equilibrium (Escobedo-Galván et al 2016). Higher temperatures produce a greater proportion of males, whereas lower temperatures produce more females (Deeming and Ferguson 1989; González et al. 2019). Counter-intuitively, the highest tolerable incubation temperatures produce mostly females, although these frequently fail to thrive (Marco et al. 2017). TSD was proposed as a possible buffer to extinction by Woodward and Murray (1993). Harsh environmental conditions are usually associated with a fall in ambient temperatures, and in species that utilise TSD these can result in a female-biased primary sex ratio (Tomillo et al. 2014;

2015; Carter et al. 2018). While lower temperatures may be consistent with the initial 'nuclear winter' effect of the end-Cretaceous bolide impact (Vellekoop et al. 2014; 2016), the longer-term warming resulting from increasing atmospheric greenhouse gas concentrations (Harrington 2001; Turner 2018) would be expected to skew sex ratios in favour of males. The latter scenario has been hypothesised as the most likely outcome of current trends in global warming (Miller et al. 2004). Although TSD has been well documented within crocodylian species (Ferguson and Joanen 1982; Deeming 2004; Piña et al. 2007), no comparisons of the effects of threshold temperature on development have been attempted across species, and little is known concerning the interrelationships between crocodylian reproductive characters.

The reproductive characters of crocodylians were first surveyed by Thorbjarnarson (1996). This work identified allometric relationships between egg mass, clutch size, clutch mass and female length: patterns that had previously been observed in other vertebrate groups (Rohwer 1988; Sinervo and Licht 1991; Shine 1992). However, the correlations and causal interactions between these reproductive variables were not the focus of this study.

Here, we used generalised linear models (GLMs) to test the relationships between the latitudinal distribution of extant crocodilian taxa and a variety of their important reproductive variables. We also tested whether there are significant relationships *between* those reproductive variables. In the context of these findings, we highlight some key questions concerning the reproductive biology, behaviour and social systems of wild crocodylians that could be addressed by future empirical and modelling work.

Figure 1: A representation of the relationship between the mean adult female body masses of 23 species of crocodylian and their latitudinal midpoint. Silhouettes scaled to body mass. Abbreviations (Asia-Pacific): Alligator sinensis, Gavialis gangeticus, Crocodylus palustris, Crocodylus mindorensis, Crocodylus siamensis, Tomistoma schlegelii, Crocodylus porosus, Crocodylus novaeguineae, Crocodylus johnstoni. *(Americas):* Alligator mississippiensis, Crocodylus rhombifer, Crocodylus moreletii, Crocodylus acutus, Crocodylus intermedius, Caiman crocodilus, Paleosuchus trigonatus, Melanosuchus niger, Paleosuchus palpebrosus, Caiman latirostris, Caiman yacare *(Africa):* Crocodylus cataphractus, Osteolaemus tetraspis, Crocodylus niloticus. Mesticops leptorhynchus *excluded due to lack of reliable female mass data.*

2 Methods

2.1 Data Collection

We compiled data from the literature for seven morphological, environmental and reproductive variables across 24 extant crocodilian species (Appendix I). We used the species list in Grigg and Kirschner (2015) (Figure 1) and included one recently described species (*Mecistops leptorhynchus*) (Shirley 2018). Recent taxonomic uncertaintly makes the attribution of some reproductive data unclear, and two species (*Crocodylus suchus* and *Osteolaemus osborni*) were

therefore excluded (Shirley et al. 2014; Hallmann and Griebeller 2018; Isberg et al. 2019). The data compiled were:

i. Maximum latitudinal range (°)

ii. Midpoint of latitudinal range (°)

iii. Mean mass of breeding-age female (kg)

iv. Mean fresh egg weight (g)

v. Mean hatchling mass (g)

vi. Threshold incubation temperature, or the temperature at which a clutch will produce approximately 50% males and 50% females (°C). The lower (female to male) threshold was selected in this case because females are often inviable at the higher (male to female) threshold.

vii. Mean clutch size (number of eggs laid)

viii. Mean duration of incubation (days)

We reviewed the literature in Google Scholar by searching for each species individually, coupled with appropriate terms (e.g. "*Crocodylus porosus* clutch size", "*Caiman yacare* body mass"). Variations on these were used as necessary (e.g. "*Caiman yacare*"/ "*Caiman jacare*" + "body mass"/"female mass"/"weight"/"kg"). These were searched until pages returned only irrelevant results. Data were collated into a single spreadsheet (Appendix I). Continuous variables (female mass, egg mass, hatchling mass, clutch size and duration of incubation) were averaged to smooth over outlier results that be unrepresentative. The literature contains data from individual captive bred and wild caught specimens, as well as values that are themselves averages from various heterogeneous samples. This constrains the precision of our data, but we believe that there is a homogenous distribution of error. In addition, data on female mass were often derived from adults of different ages, and these were then averaged across multiple individuals and studies (Appendix I). Data on latitudinal range were taken from the IUCN Red List of threatened species (IUCN 2019).

For one species, *Tomistoma schlegelii*, there was insufficient information in the literature, and we therefore used data from our own observations. Hatchling mass data (see Appendix I) were averaged from a captive-born clutch laid at "Crocodiles of the World", Oxfordshire, UK. This clutch consisted of 17 eggs, of which 14 successfully hatched (though one infant failed to thrive and died shortly after hatching). Eggs were laid on 16th April 2016 by an imported farm-raised female measuring 2.3 m (SVL). Eggs were separated and artificially incubated at 32.6° C (three eggs), 32.0° C (five eggs), 31.5° C (five eggs) and 29.8° C (four eggs), and hatched after 92 days, 94

183 days, 95 days and 103 days, respectively. Hatchlings were weighed using a Marsden Super-SS B-
184 100 waterproof electronic scale, accurate to 0.10 g.
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187
188 2.2 Statistical analysis
189 For indicative purposes, non-phylogenetically controlled bivariate correlations between our seven
190 variables are visualised in Figure 2. These were further tested using PGLS as sensitivity
191 analyses. These results, and literature on archosaur reproduction generally and crocodylians
192 specifically was used to frame five hypotheses:
193
194 i. Adult female mass is positively correlated with latitudinal midpoint, maximum
195 latitudinal range, egg mass, hatchling mass and/ or clutch size, as in some species of
196 crocodylians (Verdade 2001; Campos et al. 2008; Murray et al. 2013) and birds (Wendeln
197 1997).
198 ii. Egg mass is positively correlated with female mass, hatchling mass and/or clutch size, as in
199 some species of crocodylians (Verdade 2001; Murray et al., 2013), birds (Wiebe and
200 Bortolotti 1995) and turtles (Wallace et al. 2006).
201 iii. Hatchling mass is positively correlated with adult female mass, latitudinal midpoint,
202 maximum latitudinal range and/or egg mass, as in some species of crocodylians (Verdade

2001; Murray et al. 2013), birds (Ricklefs 1984; Smith et al. 1993) and turtles (Roosenburg and Kelley 1996; Wallace et al. 2006).

iv. Clutch size is positively correlated with adult female mass, egg mass, latitudinal midpoint, maximum latitudinal range and/or duration of incubation, as in some species of crocodylians (Verdade 2001; Campos et al. 2008; Murray et al. 2013), birds (Erikstad et al. 1993; Monaghan et al. 1995) and turtles (Roosenburg and Kelley 1996).

v. Threshold incubation temperature is positively correlated with latitudinal midpoint, maximum latitudinal range and/or hatchling mass, as in turtles (Ewert et al. 2005).

The phylogeny of O'Brien et al. (2019) was used to produce phylogenetically-independent contrast (pic) values for each variable. These pic values (rather than our raw data) were used in the subsequent GLM analyses. This tree was constructed using multiple specimens representing each species and the tree was first pruned to remove duplicate specimens ('Alligator_mississippiensis2', 'Alligator_mississippiensis3', etc.). The first entry was kept by default in each case. Rooting and branch lengths were kept consistent with those published by O'Brien et al. (2019).

Before calculating the pic values, conspicuously non-normal continuous variables (female mass, egg mass and hatchling mass only) were log-transformed. Four species were excluded from our dataset because they were absent from the phylogeny of O'Brien et al. (2019) (*Crocodylus intermedius*, *Crocodylus moreletii*, *Caiman yacare* and *Mesticops leptorhynchos*), leaving 20 species in the final analyses. We used the Akaike Information Criterion (AIC) to identify the minimum

adequate model by backward stepwise deletion of poorly fitting variables. All models used the 'Gaussian' error family and 'identity' link function, and were implemented in the statistical software environment R, using the *GGally*, *ape* and *phytools* packages (version 3.5.3) (R Core Team 2013).

We constructed five GLMs based on the phylogenetically independent contrasts of all variables. Models 3 and 5 were produced from a modified phylogeny of 17 species, excluding *Crocodylus novaeguineae*, *Osteolaemus tetraspis* and *Tomistoma schlegelii*. This was because threshold incubation temperature data were not available for these species, and also because threshold incubation temperature was shown through our Spearman's Rank test (Figure 2) to correlate with hatchling mass (model 3), incubation duration and latitudinal values (model 5).

Model No.	Dependent variable	Independent variables
1	f.mass	Lat., egg.mass, hatch.mass, clutch.size, inc.dur
2	Egg mass	Lat, f.mass, clutch.size
3	Hatch.mass	Lat., f.mass, egg.mass, clutch.size, inc.temp, inc.dur
4	Clutch.size	Lat., f.mass, egg.mass, inc.temp.
5	Inc.temp.	Lat., egg.mass, hatch.mass, clutch.size, inc.dur

Table 1: Initial structure of GLMs analysing relationships between phylogenetically independent contrasts in the reproductive characters of extant Crocodylia. All models were conducted using the 'gaussian' error family and 'identity' link function. Abbreviations: clutch.size = mean clutch size; egg.mass = log mean fresh egg weight;

f.mass = log mean adult female body mass; hatch.mass = log mean hatchling mass; inc.dur = mean duration of incubation; inc.temp = threshold incubation temperature; lat.max = maximum latitudinal range; t.lat.= latitudinal midpoint.

3 Results

A Spearman's correlation matrix of our results is shown in Figure 2. The strongest positive correlations are between morphological reproductive characteristics (female mass vs egg mass (r_s = 0.85, $p < 0.0001$), female mass vs hatchling mass (r_s = 0.79, $p < 0.0001$), and egg mass vs hatchling mass (r_s = 0.94, $p < 0.0001$)). Other correlated traits are: (1) latitudinal midpoint vs duration of incubation (r_s = -0.60, p = 0.005); (2) female mass vs clutch size (r_s = 0.67, p = 0.002); (3) egg mass vs clutch size (r_s = 0.56, p = 0.01); (4) hatchling mass vs clutch size (r_s = 0.64, p = 0.003); (5) maximum latitudinal range vs clutch size (r_s = 0.045, p = 0.046) (6) latitudinal midpoint vs duration of incubation (r_s = -0.60, p = 0.0055). PGLS analyses supported the following significant relationships: (1) female mass vs egg mass (p = 0.0008); (2) female mass vs hatchling mass (p = 0.0003); (3) egg mass vs hatchling mass ($p < 0.0001$); (4) latitudinal midpoint vs duration of incubation (p = 0.007); (5) female mass vs clutch size (p = 0.007); (6) hatchling mass vs clutch size (p = 0.015) and (7) latitudinal midpoint vs duration of incubation. Some relationships were not supported by PGLS analysis: (1) egg mass vs clutch size (p = 0.071); (2) maximum latitudinal range vs clutch size (p = 0.121).

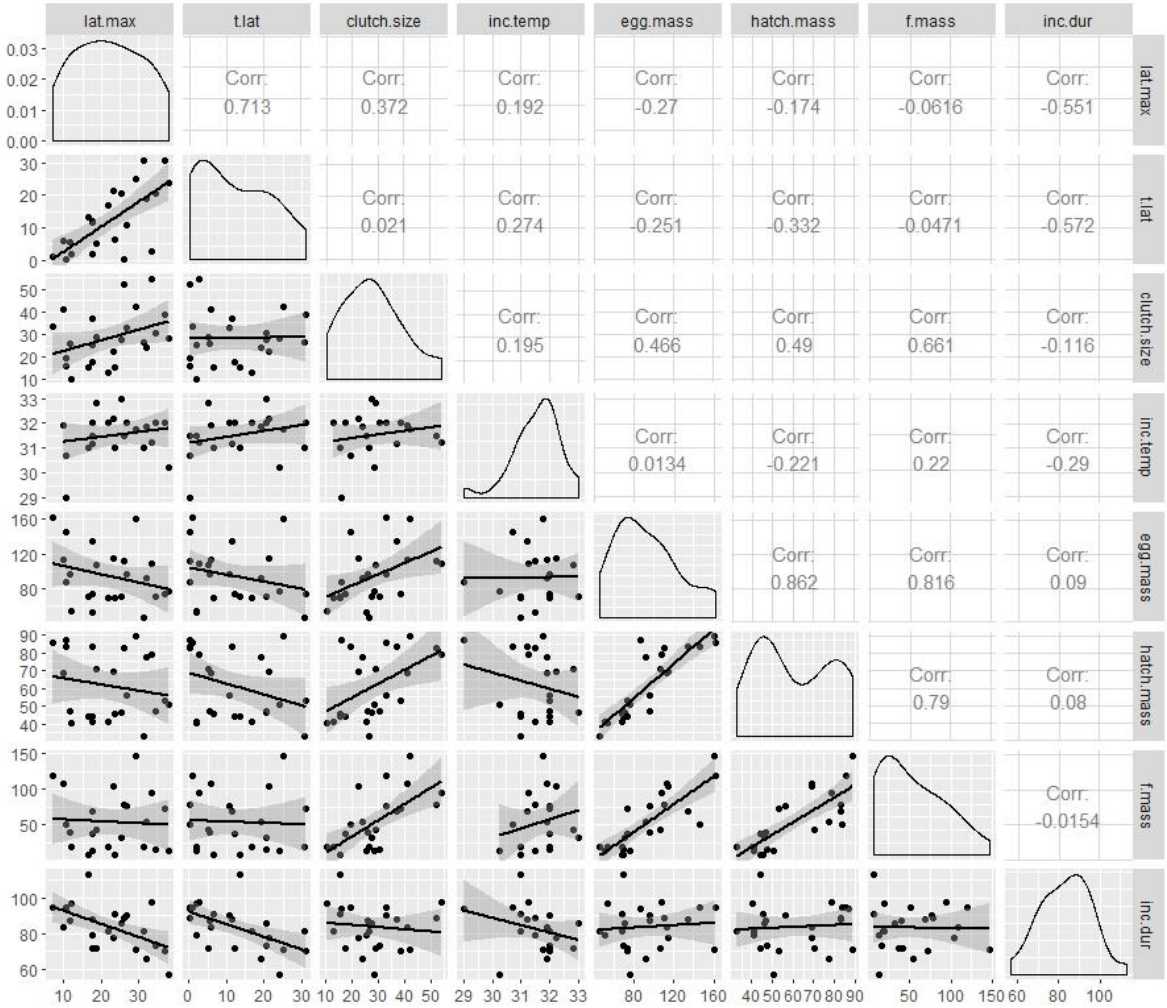

Figure 2: Spearman's correlation matrix indicating positive correlations between morphological reproductive traits (female mass, egg mass, hatchling mass), and negative correlations between latitudinal midpoint, threshold incubation temperature and incubation duration. Abbreviations: clutch.size = mean clutch size; egg.mass = log mean fresh egg weight; f.mass = log mean adult female body mass; hatch.mass = log mean hatchling mass; inc.dur = mean duration of incubation; inc.temp = threshold incubation temperature; lat.max = maximum latitudinal range; t.lat.= latitudinal midpoint

3.1 Female Mass

Model 1 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, egg mass, hatchling mass, clutch size and duration of incubation on female mass (Appendix II - initial and final models). The final model (Table 2) was the result of backward stepwise deletion based on AIC value as a measure of model efficiency. This model explained 85% of the deviance associated with adult female mass (D^2). Mean clutch size ($p = 0.0017$) was the most significant correlator to log mean female mass, followed by mean latitudinal range ($p = 0.026$), log mean hatchling mass (0.0027) and maximum latitudinal range ($p = 0.0133$). Log mean egg mass and mean incubation duration both correlated poorly with log mean female mass and were dropped from the model.

Term	Coefficients	SE	F	p
t.lat	0.0421	0.0115	13.311	0.0026**
lat.max	-0.0365	0.0129	8.0132	0.0133*
log.hatch	1.1638	0.3206	13.175	0.0027**
clutch.size	0.0348	0.0090	15.047	0.0017**

Table 2: A Generalised Linear Model (Model 1) describing the effect of latitudinal midpoint, maximum latitudinal range, hatchling mass and clutch size on the adult female mass of 20 species of crocodylian. $D^2 = 0.8510$ *SE = Standard error; F = F-value, p = p-value.*

3.2 Egg Mass

Model 2 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, female mass and clutch size on egg mass (Appendix II). The final model (Table 3) explained 68% of the deviance associated with egg mass (D^2). Log mean female mass ($p < 0.0001$) was the only significant correlator to log mean egg mass. Latitudinal midpoint and mean clutch size correlated poorly with log mean egg mass and were dropped from the model.

Term	Coefficients	SE	F	p
max.lat	-0.0074	0.0049	1.9114	0.1858
log.f.mass	0.5117	0.0809	33.295	<0.0001***

Table 3: A Generalised Linear Model (Model 2) describing the effect of maximum latitudinal range and adult female mass on the fresh egg weight of 20 species of crocodylian. $D^2 = 0.6776$. SE = Standard error; F = F-value, p = p-value.

3.3 Hatchling Mass

Model 3 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range female mass, egg mass, clutch size, threshold incubation temperature and incubation duration on hatchling mass (Appendix II). The final model (Table 4) explained 90% of the deviance associated with hatchling mass (D^2). Log mean egg mass ($p < 0.0001$) was the only significant correlator to hatchling mass. Log mean female mass, latitudinal midpoint, mean clutch size and mean incubation duration correlated poorly with hatchling mass and were

dropped from the model.

Term	Coefficients	SE	F	p
lat.max	0.0052	0.0032	2.6903	0.1269
log.egg.mass	0.8348	0.0841	98.483	< 0.0001***
inc.temp	-0.0751	0.0505	2.2103	0.1629

Table 4: A Generalised Linear Model (Model 3) describing the effect of female body mass and fresh egg weight on the hatchling mass of 17 species of crocodylian. $D^2 = 0.8997$. *SE = Standard error; F = F-value, p = p-value.*

3.4 Clutch Size

Model 4 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, female mass, egg mass and hatchling mass (Appendix II). The final model (Table 5) explained 87% of the deviance associated with clutch size (D^2). The most significant correlators to mean clutch size were log mean female mass ($p < 0.0001$) and maximum latitudinal range ($p < 0.0001$), followed by latitudinal midpoint ($p = 0.0007$) and mean duration of incubation ($p = 0.107$). Egg mass and hatchling mass were found to correlate poorly with clutch size, and were dropped from the model.

Term	Coefficients	SE	F	p
log.f.mass	11.9056	2.0480	33.796	<0.0001 ***
t.lat	-0.8362	0.1955	18.291	0.0007***

lat.max	1.0462	0.1804	33.623	<0.0001***
inc.dur	0.2435	0.1414	2.9650	0.1071 *

Table 5: A Generalised Linear Model (Model 4) describing the effect of adult female mass, latitudinal midpoint, maximum latitudinal range and incubation duration on the clutch sizes of 20 species of crocodylian. D^2 = 0.8662. *SE = Standard error; F = F-value, p = p-value.*

3.5 Threshold Incubation Temperature

Model 5 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, female mass, egg mass, hatchling mass, clutch size and incubation duration on threshold incubation temperature (Appendix II). The final model (Table 6) explained 42% of the deviance associated with threshold incubation temperature (D^2). The only significant correlator to threshold incubation temperature was mean incubation duration (p = 0.0065). Log mean female mass, log mean egg mass, log mean hatchling mass, mean clutch size, latitudinal midpoint and maximum latitudinal range all correlated poorly with threshold incubation temperature and were dropped from the model.

Term	Coefficients	SE	F	p
inc.dur	-0.0260	0.0081	10.201	0.0065**

Table 6: A Generalised Linear Model (Model 5) describing the effects of maximum latitudinal range, fresh egg weight, hatchling mass and duration of incubation on the threshold incubation temperature of 17 species of crocodylian. D^2 = 0.4215 *SE = Standard error; F = F-value, p = p-value.*

4 Discussion

4.1 General overview

A robust, positive correlation between latitude and body size has been well documented in endotherms (Gillman et al. 2009; Torres-Romero et al. 2016), but is much less compelling among ectotherms (Ashton and Feldman 2003; Lindeman 2008; Cruz et al. 2005), and has never been tested for in crocodylians. Here, we demonstrate that, despite low overall correlation coefficients, both latitudinal midpoint and maximum latitudinal range correlate significantly with adult female mass once the effects of phylogeny and other potentially confounding reproductive variables are controlled for ($p = 0.0026$ and 0.0133 respectively, see Model 1, section 3.1). Furthermore, we describe significant relationships between some important morphological reproductive variables across crocodylians as a whole, a phenomenon that has previously been described only within species (Verdade 2001; Campos et al. 2008; Murray et al. 2013). We demonstrate that these relationships are discrete with, for example, a significant effect of female mass on egg mass, and of egg mass on hatchling mass, but no direct effect of female mass on hatchling mass. Female mass is a significant predictor of clutch size in crocodylians, as well as both the latitudinal midpoint and maximum latitudinal range. We did not detect any significant relationship between threshold incubation temperature and either latitudinal midpoint or maximum latitudinal range (see Model 5, section 3.5). Some of the most biologically significant relationships described by our models are presented in Figure 3.

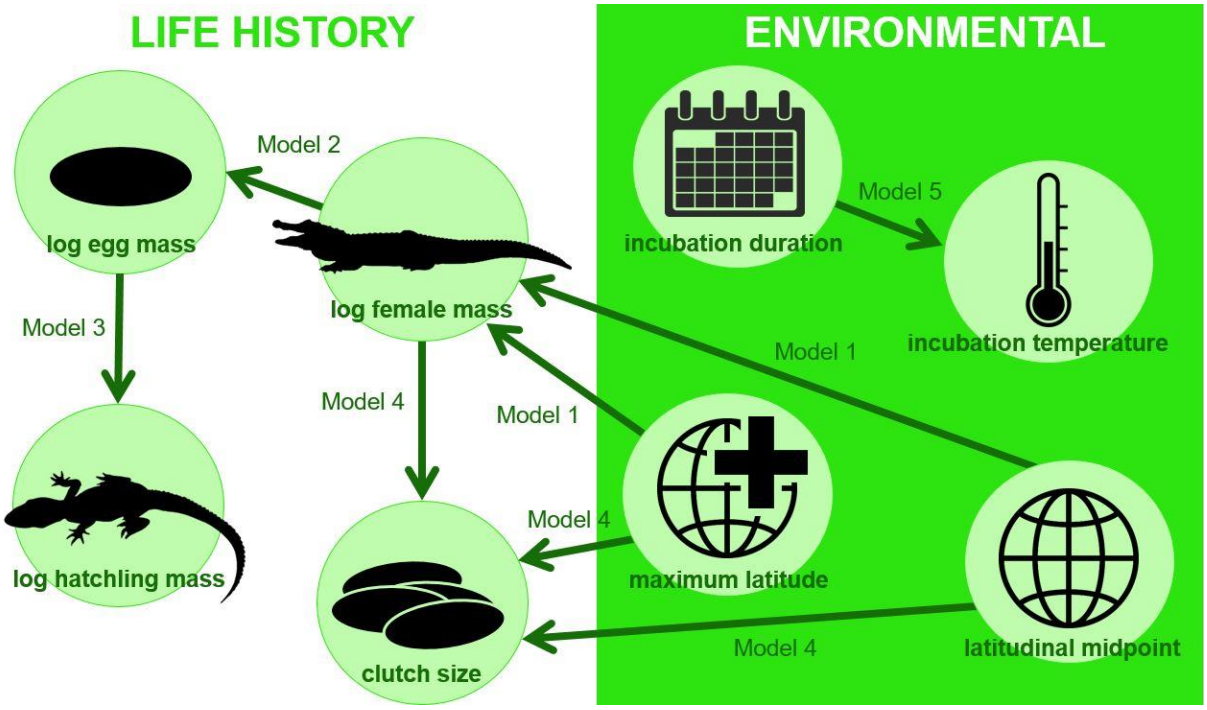

Figure 3: Map of the interactions between some important reproductive variables in Crocodylia. Positive relationships shown are between latitudinal midpoint and log mean female mass ($p = 0.0026$); maximum latitudinal range and log mean female mass ($p = 0.013$); log mean egg mass and log mean female mass ($p < 0.0001$); log mean egg mass and log mean hatchling mass ($p < 0.0001$); log mean female mass and mean clutch size ($p < 0.0001$; maximum latitudinal range and mean clutch size ($p < 0.0001$); latitudinal midpoint and mean clutch size ($p = 0.0007$); and mean incubation duration and threshold incubation temperature ($p = 0.0065$).

4.2 Implications of results

The strongest associations in our study are between morphological reproductive variables (Models 1, 2 and 3). These include adult female mass, fresh egg weight, hatchling mass and clutch size (Figure 3). Intraspecific relationships of this kind have previously been documented in the

362 American alligator (*Alligator mississippiensis*) (Murray et al. 2013) and in the broad-snouted,
363 spectacled and Yacare caimans (*Caiman latirostris*, *C. crocodilus* and *C. yacare*) (Verdade 2001;
364 Larriera et al. 2004; Campos et al. 2008). Here, we verify the same trends across extant
365 crocodylians as a whole. We report a significant positive effect of female mass upon clutch size
366 (Model 4), a result that contrasts with the findings of previous species-level studies (Verdade
367 2001). We find no evidence for any correlation between egg mass and clutch size, which is a
368 biological trade-off that has been described in many other taxa (Lack 1967; Sinervo and Licht 1991;
369 Rowe 1994).
370
371 We found no significant relationship between threshold incubation temperature and hatchling
372 mass (Models 3 and 5), suggesting that the temperature required to produce an even sex ratio is
373 not significantly different in crocodylian species that produce large hatchlings compared with
374 those that produce small hatchlings. This result is consistent with previous studies that
375 examined trends within species (Joanen and McNease 1989; Campos 1993). The effects of
376 contemporary climatic warming on the reproductive biology of crocodylians has yet to be
377 examined (Zhang et al. 2009; Simoncini et al. 2014), but based on deep-time associations
378 between crocodylian distributions and climate change (Markwick 1998; Quintero and Wiens
379 2013; Mannion et al. 2015), it is plausible that all crocodylians are vulnerable to rapid warming,
380 and that this should be considered a threat to local populations (Dudgeon 2014).
381
382 Our results suggest that the only significant correlator to threshold incubation temperature in

crocodylians is incubation duration (Model 5). This factor may help to explain the diversity of threshold incubation temperatures as, within species, eggs incubated at higher temperatures tend to hatch sooner than those incubated at cooler temperatures (see section 2.1 on *Tomistoma schlegelii*, Methods).

We identified no significant relationships between the threshold incubation temperature and either the mean or the maximum latitudinal range of crocodylians (Model 5). This suggests that the nest temperature of crocodylians is affected by factors other than latitudinal distribution. This stands in contrast to the relationship observed in turtles, in which latitude has a significant effect on reproductive traits and nest temperature (Iverson et al. 1993; Ewert et al. 2005). The clutch size of turtles correlates with latitude (Iverson et al. 1993) and their sex ratio is affected by annual temperature fluctuations (Janzen 1994). This supports observed differences in the nest functions and parental roles of turtles and crocodylians, and suggests that the presence of adult crocodylians at the nest plays a much greater role in the temperature regulation of their nests than in turtles. Our results suggest that other factors (possibly the position, construction, location, shape or size of the nest) could contribute to the maintenance of an acceptable nest temperature (see also Grigg 1987, Brazaitis and Wantanabe 2011). In turtles, nest temperature is determined by ambient temperature and climate to a much higher degree (Hays et al. 2010; Refsnider et al. 2013; Santidrián et al. 2015). Future research on the behaviour of nesting crocodylians may be necessary to shed further light on nest temperature regulation.

4.3 Limitations and future work

We note that some sources in the literature measured female mass at first laying, while others measured older females. Because crocodylians grow consistently post sexual maturity (Seymour et al. 2013), this could produce variable results. While our data were means from all of the published studies we were able to identify, we recognise the limitations of literature-based data collection, and acknowledge that the standardized collection of primary data would be preferable. This use of species mean values for mass, latitudinal distribution and clutch size also masks both population level and biogeographical variation (Simoncini et al. 2009). Gathering these additional data would offer greater power, and enable both within- and cross-species comparisons.

An extension of the present study could include additional parameters such as nest dimensions, nest humidity, geographic range, and postcopulatory reproductive behaviours (nest defence, guarding of hatchlings, etc.) to test the influence of these on crocodylian distribution and behaviour.

Mortality rates among unguarded eggs and hatchlings have been suggested as factors that may promote selection for parental care (Klug and Bonsall 2010; Klug et al. 2012). Since there seems to be a wide within-species range of parenting behaviours in crocodylians (Hunt and Watanabe 1982; Platt et al. 2008), the group is a good model system for investigating the effects of different types of care. For example - do female crocodylians living in high-stress

environments (at the edge of their range or in human-dominated landscapes) exhibit the same rates and types of parenting behaviour as those living in highly protected habitats? This represents an interesting subject for future research, especially as the habitats of crocodylians are increasingly subject to human encroachment and climatic stress (Langley 2005; Amarasinghe et al. 2015; Corvera et al. 2017).

5 Conclusions

We present the first evidence for a latitudinal effect on the body size of extant crocodylian species (as adults and hatchlings) and make the novel observation that major reproductive characteristics of extant crocodylians follow a consistent pattern of effect across the entire order.

We report no significant relationship between either latitudinal midpoint or maximum latitudinal range and threshold incubation temperature across sampled crocodylians. This contrasts markedly with the patterns seen in turtles and raises additional questions about the parental roles of crocodylians. Further work will be needed to clarify the possible responses of crocodilian reproduction and its impact on their resiliance in relation to anthropogenic warming. This may have implications for future studies on the effects of climate, latitude and life history on ectothermic amniotes, and for conservationists and government departments responsible for legislating on wildlife protection and climate change mitigation strategies.

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